

MOTILE MACROEPIFAUNA OF THE SEAGRASSES, *AMPHIBOLIS* AND *POSIDONIA*, AND UNVEGETATED SANDY SUBSTRATA IN HOLDFAST BAY, SOUTH AUSTRALIA

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Summary

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The motile macroepifauna was examined in stands of *Amphibolis antarctica*, in mixed stands of *Posidonia angustifolia* and *Posidonia sinuosa*, and in nearby unvegetated sand at two sites in Holdfast Bay, South Australia. In all, 178 species including 49 species of molluscs and 114 species of crustaceans were recorded in the three habitats. There were significantly more species at both sites, and significantly more individuals at one site, in vegetated than unvegetated substrata. Seagrass biomass was significantly and positively correlated with the number of species and number of individuals at the shallow site, but not at the deeper one. Seagrass biomass appears to be only one of a number of factors determining the structure of the macroepifaunal assemblage. Cluster analyses of samples show that the faunas of each habitat are distinct. Of the 25 most common species, 11 were significantly associated with *Amphibolis*, eight with *Posidonia*, and six were associated with vegetated as compared with unvegetated substrata, with which five were associated. Only harpacticoid copepods of the genus *Amphiascopsis* were non-selective. The habitat preferences of species appear to be a complex result of individual requirements for food and shelter.

KEY WORDS: macroepifauna, seagrasses, molluscs, crustaceans, *Posidonia*, *Amphibolis*, South Australia.

Introduction

Seagrasses are a conspicuous element in temperate Australian coastal waters (Larkum 1977; Womersley 1984) and especially important in the South Australian Gulfs where they form extensive meadows (Shepherd & Sprigg 1976; Shepherd 1983; Thomas & Clarke 1988) and might be expected to provide a large fraction of the total productivity (Mann 1982). Seagrasses also provide habitat, shelter and food for many mobile invertebrates which in turn are used as food by fish and other secondary consumers (Kikuchi 1974; Robertson 1980; Pollard 1984 and reviews by Virnstein 1987; Howard *et al.* 1988; Bell & Pollard 1988). Invertebrates are thus an important link in the trophic network in coastal seagrass communities. Because the seagrass beds in Holdfast Bay, South Australia have become seriously degraded (see Clarke 1987, and review by Shepherd *et al.* 1988) the consequences of such loss on higher trophic levels needs to be assessed.

This study was of a pilot nature and set out to describe the motile macroepifauna of two major seagrasses and unvegetated substrata, and so document the faunistic changes that might be expected to result from the decline of seagrasses in Holdfast Bay. The seagrasses were *Posidonia angustifolia* Cambridge & Kuo and *P. sinuosa* Cambridge & Kuo, which occur in mixed stands, and *Amphibolis antarctica* (Labillardiere) Sonder & Ascherson ex

Ascherson. The unvegetated substrata were blow-outs, which occur widely in these seagrass beds (Fig. 1 a). *P. angustifolia* and *P. sinuosa* are similar to each other morphologically, both having long narrow blades arising from a rhizome, and can be readily distinguished only by examination of the buried sheath or (microscopically) of the epidermal cells (Cambridge & Kuo 1979). *A. antarctica* is architecturally more complex with a tough cylindrical stem supporting an array of tufted leaves.

We examined the species composition and abundance of all taxa retained in a 1 × 0.5 mm mesh in vegetated areas over a range of seagrass biomass values and in unvegetated sandy areas in order to assess the importance of the structure and biomass of these seagrasses to the macroepifauna. In each case epifaunal, but not infaunal, taxa associated with the substratum were sampled.

Because the macroepifauna is highly mobile and might be expected to select an optimal habitat, based on seagrass architecture and density, and because survival may differ between habitats and within habitats according to seagrass density, differences in epifaunal species composition and abundance should disclose the net outcome of these two processes, i.e. habitat preferences and differential survival.

An important collateral aim of the study was to obtain a taxonomic reference collection of macro-invertebrate taxa associated with seagrass and unvegetated substrata in Holdfast Bay for use in later studies. Voucher specimens are lodged in the South Australian Museum. Except for the study of Watson *et al.* (1984) on *Heterozostera* this has not

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previously been attempted for southern Australian seagrasses.

Materials and Methods

Study Sites

Sites were selected in Holdfast Bay, S. Aust., where serious seagrass recession has occurred through expansion of blowouts and the effects of sewage sludge effluent (see Shepherd *et al.* 1988). One study area (Blowouts S1 and S2) was located 1.4 km off Henley Beach (34°55.5'S, 138°30'E) at 6–7 m depth (Fig. 2) where extensive mixed stands of *Posidonia angustifolia* and *P. sinuosa*, and smaller patches of *Amphibolis antarctica* surround

blowouts. The second study area (Blowout S3), examined at a later date, was 2.6 km off Brighton (35°01'S, 138°31'E) at 10–11 m depth where *P. angustifolia* is dominant and *A. antarctica* occurs only in small patches. The former area was chosen because it was considered to be representative of seagrass habitats in Holdfast Bay; this judgement was based on extensive sampling during comprehensive studies of seagrass-sediment dynamics of Holdfast Bay (Clarke 1987; Thomas & Clarke 1988). The latter area was near the maximum depth of seagrass and was chosen to maximise contrast with the former, and so test the applicability of the earlier results to a deeper seagrass habitat.



Fig. 1. (a) Aerial photograph at Brighton in Holdfast Bay showing blowouts in seagrass beds. Bar scale 500m. (b) Diver sampling unvegetated substratum in a blowout. (c) Oblique view of *Amphibolis* bed. (d) Oblique view of *Posidonia* bed.

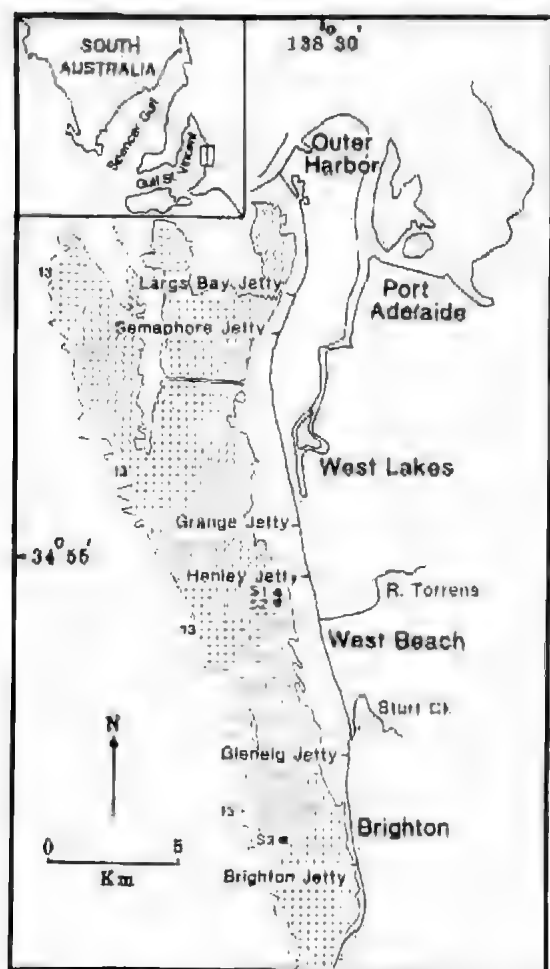


Fig. 2. Holdfast Bay, South Australia showing study sites and seagrass distribution.

A 25 × 25 cm quadrat frame attached to the open end of a plankton net of mesh size 1 × 0.5 mm and enclosing a volume of 40 litres was used for sampling. The net was secured to the quadrat by a lace and unfolded only when the quadrat was rapidly thrust downwards to the seabed during the sampling operation (Fig. 1 b, c, d). All samples, both in vegetated and unvegetated areas, were taken about 5 m from the seagrass-sand boundary of the blowout being investigated, in order to avoid possible 'edge effects'.

In the seagrass samples, the seagrass was cut off at sand level with shears operated from outside the net. After the sample was taken, the net was released from the quadrat, the surficial sediment was manually disturbed to a depth of 1–2 cm in order to expel sheltering animals into the water column, the opening tied shut, and the net and con-

tents sealed in a plastic bag. The technique is similar to that described by Ledoyer (1962) and used by Scipione & Fresi (1984), Virnstein *et al.* (1984) and others.

At the Henley Beach site six replicate samples were taken in each of three habitats (unvegetated sand, *Posidonia* and *Amphibolis*) at two blowouts (S1, S2) giving 36 samples in all. At Brighton eight replicates were taken in the same three habitats at one blowout (S3) giving 24 samples.

Samples, including the surficial sediment and any detritus, were preserved in 10% formalin and seawater and later hand-sorted to remove all animals. The seagrass in each sample was weighed after removal of excess water, and animals were identified to the lowest possible taxon and species' abundances per quadrat tabulated. Sampling was done at about noon, in March 1985 at S1 and S2 and in November 1985 at S3.

Only the motile macroepifauna is considered here. Bryozoans, foraminiferans, hydroids and polychaetes, and meiofaunal species not adequately retained by the mesh, are excluded.

Analyses

Data for the two sites cannot be compared directly due to differences in depth and time of sampling and in locality, and are analysed separately.

A cluster analysis of species' abundances per quadrat was performed on the data from each site. After a log (N + 1) transformation of the data the Euclidean distance measure of similarity and the group average sorting strategy were used to achieve clustering of quadrat data (see Clifford & Stephenson 1985; Field *et al.* 1982).

Data on number of species and number of individuals were examined by analysis of variance (ANOVA). Where the variances are heterogeneous, as disclosed by a Cochran C-test, data were transformed to achieve homogeneity. A Student–Newman–Keuls (SNK) test was then used to detect significant differences between individual means. Cluster analyses, ANOVAs and least squares regressions were performed with the Biostat computer package (R. A. Pimental & J. D. Smith 1985; Sigma Soft Placentia, California).

Results

Community Totals

In all, 7124 individuals divided among 178 species were obtained in the two vegetated habitats (*Amphibolis* and *Posidonia*) and in unvegetated sand. There were 49 species of molluscs, 114 species of crustaceans (59 amphipods, 19 isopods, 13 decapods, five mysids, ten copepods and eight ostracods), seven species of pycnogonids and eight

species of echinoderms. The species with authorities are listed in Table 1.

Analyses of variance show that the number of species differs significantly between seagrass habitat and unvegetated sand at both sites (Tables 2, 3). At the Henley Beach site there is no significant difference ($P > 0.05$) between the two blowouts (S1, S2). There are significantly fewer species in unvegetated sand than in seagrass at both sites, but no significant difference in number of species between the two seagrasses (Table 3). Overall, there are fewer species of molluscs than of arthropods in seagrass, except that at Brighton there is little difference in the number of species of mollusc between unvegetated sand and *Posidonia* (Fig. 3).

The two sites do not give a consistent picture in the variation in number of individuals per sample in relation to habitat. At Henley Beach there is no significant ($P > 0.05$) difference between any habitat, but at Brighton there are significantly fewer individuals in *Posidonia* and sand than in *Amphibolis* (Table 3).

Next we examined by regression analysis the role of seagrass biomass as a factor influencing the number of species and of individuals per sample. Significant linear regressions relating number of species and individuals with *Posidonia* and *Amphibolis* biomass respectively are given in Table 4 for Henley Beach. Here the number of species in *Posidonia* and both number of species and individuals in *Amphibolis* are significantly related to biomass; at Brighton there are no significant regressions.

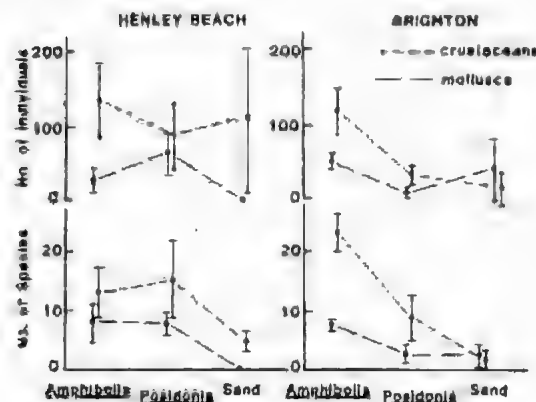


Fig. 4. Mean number of individuals and species of crustaceans and molluscs per sample in three habitats, (*Amphibolis*, *Posidonia* and unvegetated sand) at Henley Beach and Brighton. Vertical bars are standard errors.

Habitat differences

Dendrograms of sample classifications using species abundances as attributes (Fig. 4) show that, with minor exceptions, the vegetated habitats, *Posidonia* and *Amphibolis*, and unvegetated sand separate out at relative similarities of less than 42%, indicating faunistic coherence within, and substantial dissimilarity between, habitats. At Henley Beach, the epifaunas of *Posidonia* and *Amphibolis* are relatively distinct and more similar to each other than either is to sand, whereas at Brighton there is greater similarity between the fauna of unvegetated sand and *Posidonia*. In fact one *Posidonia* sample was more similar to sand samples than to other *Posidonia* samples, due to the absence of the harpacticoid *Porcellidium* sp which was generally common in seagrasses but rare in sand (Table 5).

Pie diagrams (Fig. 4) show the mean relative abundances of molluscs and arthropods for each habitat; they indicate strong dominance by a few species with a very large number of rare species. The 25 most common species (i.e. those with mean relative abundance per habitat of $>5\%$) differ significantly in their absolute abundances between the three habitats, and are categorised according to their apparent preferences (Table 4). Eleven of the 25 species are more abundant in *Amphibolis*, two species are more abundant in *Posidonia*, and six species are more abundant in both seagrasses without distinction between them. Only the harpacticoid *Amphiscopsis* spp are indifferent to habitat; but this has little significance since several taxa may be included.

There are very marked differences between the faunas of the two sites, Henley Beach and Brighton. Fourteen of the 25 most common species, and 76% of all species occur only at one site.

Unvegetated blowouts have a characteristic fauna which differs between the two sites. At Henley Beach the amphipod *Guernia cf. gelana* and the ostracod *Cypridinodes galathea* are dominant, and at Brighton the minute gastropod *Lixostoma contabulata*, the harpacticoid *Amphiscopsis* spp, the mysid *Leptomysis australis*, the tanaid *Leptochelia ignota* and the sea-star *Allostichaster polyplax* are co-dominant (Fig. 4).

Discussion

Despite the very limited sampling program that could be carried out in this study, some comparison can still be made with the species richness of seagrass epifauna elsewhere. Virnstein *et al.* (1984) have assembled comparative data on species abundances of amphipods, isopods and decapods in

TABLE 1. List of species with authorities obtained in the study.

Phylum MOLUSCA	
Class GASTROPODA	
Trochidae	<i>Badepyrus pupoides</i> (Adams) <i>Thalotia conica</i> (Gray) <i>Cantharidus irisodontes</i> (Quoy & Gaimard) <i>Cantharidus bellulus</i> (Dunker) <i>Cantharidus apicinus</i> (Menke) <i>Nanula</i> sp. <i>Calliostoma</i> sp. <i>Calliostoma legrandi</i> (Tenison Woods) <i>Calliostoma hedleyi</i> Pritchard & Gatliff <i>Callistele calliston</i> (Verco) <i>Ethminolia elveri</i> Cotton & Godfrey
Fissurellidae	<i>Macroschisma tasmaniae</i> Sowerby <i>Notoacmea flammea</i> (Quoy & Gaimard)
Lioliidae	<i>Argalista</i> sp. <i>Lissotesta contabulata</i> Tate
Patellidae	<i>Patella (Scutellastra) peronii</i> Blainville
Phasianellidae	<i>Phasianella australis</i> (Gmelin)
Turritellidae	<i>Gazameda iredalei</i> Finlay
Epitonidae	<i>Acutiscata minora</i> Iredale
Calyptraeidae	<i>Calyptraea calyptraeformis</i> (Lamarck)
Melanellidae	<i>Curveulima indiscreta</i> (Tate)
Potamididae	<i>Batillaria bivaricata</i> Ludbrook <i>Batillaria diemenensis</i> (Quoy & Gaimard)
Cymatiidae	<i>Cymatella gaimardi</i> Iredale
Vermetidae	<i>Tenagodus weldii</i> Tenison Woods
Columbellidae	<i>Mitrella acuminata</i> (Menke)
Olividae	<i>Oliva australis</i> Duclos
Fasciariidae	<i>Microcolus dunkeri</i> (Jonas)
Pyrenidae	<i>Macrozofra atkinsoni</i> (Tenison Woods)
Nassariidae	<i>Niutha pyrrhus</i> (Menke)
Triphoridae	<i>Hedleytriphora scitula</i> (A. Adams)
Muricidae	<i>Bedevea paivae</i> (Crosse) <i>Lepsiella flindersi</i> (Adams & Angas)
Buccinidae	<i>Cominella eburnea</i> (Reeve)
Triphoridae	<i>Obesula albobittata</i> (Hedley)
Pyramidellidae	<i>Congulina</i> sp. <i>Pyrgiscus</i> sp. <i>Chemnitzia mariae</i> (Tenison Woods) <i>Odostomia</i> sp. <i>Acteocina fusiformis</i> (A. Adams)
Scaphandridae	
Class BIVALVIA	
Glycymeridae	<i>Glycymeris radians</i> (Lamarck)
Mytilidae	<i>Musculus paulucciae</i> Crosse <i>Trichomusculus penetectus</i> (Verco)
Pteriidae	<i>Electroma georgiana</i> (Quoy & Gaimard)
Veneridae	<i>Tawera lagopus</i> (Lamarck)
Psammobiidae	<i>Gari brazieri</i> Tate
Class AMPHINEURA	
Ichnochitonidae	<i>Stenochiton cymodacealis</i> Ashby <i>Stenochiton pilsbryanus</i> Bednall
Class CEPHALOPODA	
Idiosepiidae	<i>Idiosepius notoides</i> Berry
Phylum CRUSTACEA	
Amphipoda	
Corophiidae	<i>Corophium</i> sp.1 <i>Corophium</i> sp.2 <i>Corophium</i> sp.3 <i>Corophium</i> sp.4 <i>Erichthonius</i> sp.
Ochlesidae	<i>Ochlesis eridunda</i> Barnard
Cypridinidae	<i>Austropehonoides mundoe</i> Barnard <i>Cyproidea ornata</i> Haswell <i>Naeapheonoides mullaya</i> Barnard

Caprellidae	<i>Caprella scaura</i> (Templeton) <i>Caprella danilevskii</i> (Czerniavskii) <i>Paraproto spinosa</i> (Haswell)
Corophilidae	<i>Cerapus abdictus</i> (Templeton)
Prophiantinae	<i>Guernea</i> c.f. <i>gelane</i> Barnard
Liljeborgiidae	<i>Liljeborgia</i> sp.
Phoxocephalidae	<i>Brolgus tattersalli</i> (Barnard) <i>Cunmurra itickerus</i> Barnard <i>Matong matong</i> Barnard <i>Birubius</i> sp.1 <i>Birubius</i> sp.2 <i>Birubius wirakus</i> Barnard <i>Birubius</i> c.f. <i>chintoo</i> Barnard <i>Booranus wangoorus</i> Barnard <i>Urohaustorius</i> sp. <i>Urothoides</i> sp.
Haustoriidae	<i>Paradexamine goomai</i> Barnard <i>Paradexamine</i> c.f. <i>guarallia</i> Barnard <i>Paradexamine thadalee</i> Barnard <i>Paradexamine</i> c.f. <i>windarra</i> Barnard <i>Paradexamine frinsdorfi</i> Sheard <i>Paradexamine moorhousei</i> Sheard <i>Paradexamine</i> sp.
Dexaminidae	<i>Atylus homochir</i> Haswell <i>Amaryllis macrophthalma</i> Haswell <i>Tryphosella orana</i> Barnard <i>Tryphosella</i> spp. <i>Parawaldeckia</i> spp. <i>Parawaldeckia stebbingi</i> (Thomson) <i>Parawaldeckia yamba</i> Barnard
Lysianassidae	<i>Maera viridis</i> Haswell <i>Ceradocus</i> sp. <i>Mallacoota carteta</i> Barnard <i>Mallacoota subcarinata</i> Haswell <i>Cymadusa variata</i> Sheard <i>Cymadusa filosa</i> Savigny
Gammaridae	<i>Leucothoe commensalis</i> Haswell <i>Leucothoe</i> sp.
Ampithoidae	<i>Gitanopsis</i> sp.
Leucothoidae	<i>Aora typica</i> Kroyer <i>Atylus</i> sp.
Amphiloichidae	<i>Tethygeneia megalophthalma</i> (Haswell) <i>Tethygeneia</i> sp.
Aoridae	sp.1
Atylidae	<i>Podocerus</i> sp.
Eusiridae	<i>Ausatelson kolle</i> Barnard <i>Ausatelson ule</i> Barnard
Phliantidae	<i>Serolis levidorata</i> Harrison & Poore <i>Serolina deluvia</i> Poore
Podoceridae	
Stenothoidae	
Serolidae	
Isopoda	
Sphaeromatidae	sp.1 <i>Exosphaeroma</i> sp.1 <i>Exosphaeroma</i> sp.2 <i>Dynamenella</i> sp. <i>Dynamenella parva</i> (Baker) <i>Pseudocerceis</i> c.f. <i>trilobata</i> Baker <i>Haswellia emarginata</i> Haswell <i>Cymodoce coronata</i> Haswell
Cymothoidae	<i>Cirolana</i> sp. n.gen. n.sp. (see Baker 1926, p. 279, Pl. XLVII)
Anthuridae	<i>Paranthura punctata</i> (Stimpson) <i>Accalathura</i> sp. <i>Paranthura</i> sp. n.gen. n.sp.
Janiridae	sp.1
Jaeropsidae	<i>Jaeropsis</i> sp.
Arcturidae	<i>Neastacilla</i> sp. <i>Neastacilla deducta</i> (Hall)

Idoteidae	<i>Crabzyos longicaudatus</i> (S. Bate)
Tanaidacea	
Tanaidae	<i>Leptochelia ignota</i> (Chilton)
Decapoda	
Hymenosomatidae	<i>Halicarcinus ovatus</i> (Stimpson)
Crangonidae	<i>Pontophilus intermedius</i> (Fulton & Grant)
Pandalidae	<i>Parapandalus leptorhynchus</i> (Stimpson)
	<i>Crangon</i> sp.
Hippolytidae	<i>Hippolyte</i> sp.
	<i>Hippolyte tenuirostris</i> (S. Bate)
	<i>Hippolyte australiensis</i> (Stimpson)
	<i>Latreutes compressus</i> (Stimpson)
	<i>Latreutes</i> sp.
Processidae	<i>Processa</i> sp.
Paguridae	<i>Paguristes</i> sp.
Penaeidae	<i>Peneus</i> sp.
Majidae	<i>Naxia aries</i> (Guerin)
Mysidacea	
Mysidae	<i>Australomysis acuta</i> (Tattersall)
	<i>Australomysis incisa</i> G.O. Sars
	<i>Afromysis australiensis</i> (Tattersall)
	<i>Gastrosaccus indicus</i> (Hansen)
	<i>Leptomysis australiensis</i> (Tattersall)
Class COPEPODA	Calanoida
Pseudodiaptomidae	sp.1
Harpacticoida	
Porcellidiidae	<i>Porcellidium</i> sp.
	<i>Amphiascopsis</i> spp.
Harpacticidae	n.sp.
Laophontidae	sp.1
Cumacea	
Bodotriidae	<i>Cyclapsis</i> sp.
	<i>Leptocuma</i> sp.
	<i>Symphodomma bakeri</i> Hale
Dasyliidae	<i>Anchicolurus waitei</i> (Halc)
Nannastacidae	<i>Cumella laeve</i> Calman
Class OSTRACODA	
Nebaliacea	<i>Paranebalia longipes</i> (Sars)
Myodocopida	<i>Cypridinodes</i> c.f. <i>galathea</i> Poulsen
	<i>Alteratochelata</i> c.f. <i>lizardensis</i> Kornicker
	<i>Vargula</i> sp.
Cylindroleberididae	sp.1
	<i>Lowoleberis</i> sp.
Podocopida	<i>Xestoleberis</i> sp.
	<i>Neonesidae</i> sp.
Phylum CHELICERATA	
Class PYCNOGONIDA	
Ammotheidae	<i>Ascorhynchus longicollis</i> (Haswell)
	<i>Achelia</i> sp.1
	<i>Achelia</i> sp. nov.
Callipallenidae	<i>Callipallene</i> sp.
	<i>Callipallene emaciata</i> (Dohrn)
	<i>Pseudopallene</i> sp.
	<i>Propallene</i> sp. nov.
Phylum ECHINODERMATA	
Class ECHINOIDEA	
Temnopleuridae	<i>Amblypneustes oyum</i> (Lamarck)
Class CRINOIDEA	
Aporometridae	<i>Aporometra wilsoni</i> (Bell)
Class ASTEROIDEA	
Asteriidae	<i>Uniophora granifera</i> (Lamarck)
	<i>Allostichaster polyplax</i> (Muller & Troschel)
Class OPHIUROIDEA	
Ophionereididae	<i>Ophionereis schayeri</i> Muller & Troschel

Ophiacanthidae

Ophiopeza assimilis Bell
Ophiucomina australis H. L. Clark
Ophiacantha alternata A. M. Clark

TABLE 2. Analysis of variance testing differences in number of species and individuals per sample at Henley Beach and Brighton sites. *** $P < 0.001$; n.s. $P > 0.05$.

HENLEY BEACH						
No. of species			No. of individuals			
(a)	d.f.	MS	F	(b)	MS	F
Location(L)	1	0.78	1.84 n.s.		6346.8	1.11 n.s.
Habitat(H)	2	4.39	10.36 ***		4176.9	0.73 n.s.
L x H	2	19.95	47.05 ***		11348.4	1.99 n.s.
Error	30	0.42			5718.0	

BRIGHTON						
No. of species			No. of individuals			
	d.f.	MS	F		MS	F
Habitat	2	1493	128 ***		44332	42.4 ***
Error	21	12			1045	

TABLE 3. Mean number of species and individuals per sample in three habitats at the Henley Beach and Brighton sites. Standard errors in brackets. 'a' indicates no significant ($P > 0.05$) difference by SNK test.

HENLEY BEACH			BRIGHTON
Species	Blowout S1	Blowout S2	Blowout S3
<i>Amphibolis</i>	23.0 (3.0) a	21.3 (1.3) a	30.5 (1.1)
<i>Posidonia</i>	29.2 (3.4) a	22.8 (3.6) a	11.5 (1.5)
sand	6.5 (1.0)	5.5 (0.6)	4.0 (1.0)
Individuals			
<i>Amphibolis</i>	151.2 (29.9) a	168.2 (18.3) a	170.1 (10.5)
<i>Posidonia</i>	178.8 (30.0) a	136.0 (25.6) a	35.2 (5.7) a
sand	166.0 (42.7) a	81.7 (33.3) a	47.8 (16.0) a

TABLE 4. Regression equations of number of species (S) and number of individuals (I) per sample against wet weight (W) in grams of *Posidonia* and *Amphibolis* in samples at Henley Beach. (* $P < 0.05$; ** $P < 0.01$; n.s. $P > 0.05$). In each regression sample size is 12.

		Equation	R ²
Species	<i>Posidonia</i>	$S = 10.6 + 0.35 W$	0.39*
	<i>Amphibolis</i>	$S = 17.2 + 0.03 W$	0.08 n.s.
Individuals	<i>Posidonia</i>	$I = 3.9 + 3.5 W$	0.62**
	<i>Amphibolis</i>	$I = 44.5 + 0.76 W$	0.46*

seagrasses at various latitudes. Judged against this compilation, the mean number of species recorded in vegetated substrata per site for amphipods (36 species) and isopods (10 species) is higher, and that of decapods (8.5 species) is lower compared with other locations at about the same latitude (35°). Similar comparisons for molluscs are not available because of lack of uniformity in method of collecting in different places. However, Ledoyer (1966) recorded similar numbers of molluscan species in seagrass to those given here. Overall, the species richness of the epifauna in these seagrasses in Holdfast Bay is comparable with that of the

Mediterranean *Posidonia oceanica* (Ledoyer 1966) which is notably rich in species (see Virnstein *et al.* 1984). The number of species of macroepifauna in *Heterozostera* in much shallower water in Victoria (Watson *et al.* 1984) is much lower than that recorded in this study.

The faunistic coherence of habitats and the significant differences in abundance of common species between habitats suggest that there are strong associations between many epifaunal species and habitat. Two causes of these associations – species' requirements for food and for shelter – are of recognized importance.

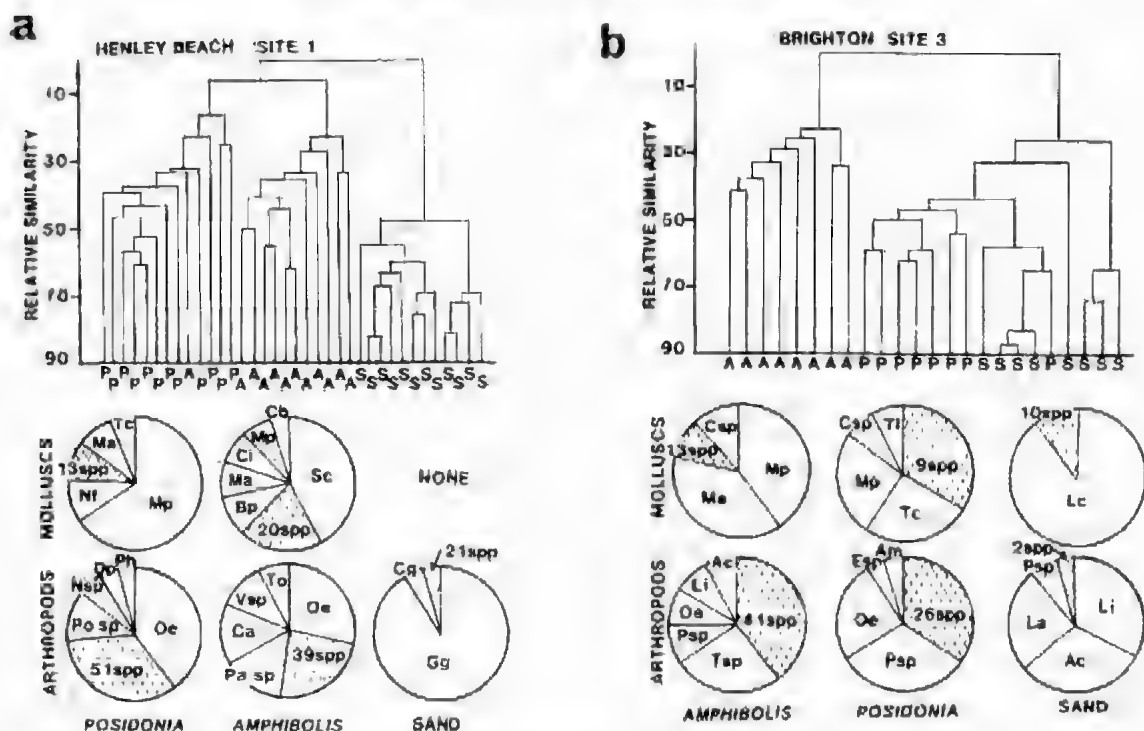


Fig. 4. Dendrograms of sample classifications for (a) Henley Beach and (b) Brighton sites, and pie diagrams of relative mean abundances of most common molluscs and arthropods in three habitats, *Amphibolis*, *Posidonia* and unvegetated sand. The key to species' abbreviations is given in Table 5.

The food requirements of species are apparent for many molluscs e.g. archaogastropods which graze on macro- or micro-algae on seagrass blades, and mesogastropods and neogastropods which are variously detritivores, carnivores or suspension feeders (Ludbrook & Gowlett-Holmes 1988). A few species are host-specific, such as the two species of *Stenochiton* (*S. pilsbryanus* on *Posidonia* and *S. cymodocealis* on *Amphibolis*), or have strict microhabitat requirements such as *Musculus paulucciae*, which occurs in the basal interstices between seagrass blades.

Similarly, many amphipods, isopods and decapods feed on seagrass epiphytes or detritus (Zimmerman *et al.* 1979; Howard 1982, 1984; Watson *et al.* 1984), and pycnogonids and some decapods are predators of smaller invertebrates (Howard 1984; Staples¹). These species are presumably linked to seagrass habitats where their food is more abundant.

The requirement for shelter in which plant architecture, biomass, surface area and density have each been emphasized (see Homziak *et al.* 1982; Stoner 1982, 1983; Lewis 1984; review by Orth *et*

al. 1984; Virnstein & Howard 1987 a, b), may also contribute to the observed association between species and habitat. However our data do not allow (nor was the purpose of this study) to distinguish between the requirements for food and shelter or assess the relative importance of each. The existence of simple linear relations between measures of plant abundance and numbers of species or individuals is consistent with hypotheses of requirements for either food or shelter. But such relations may often be obscured by the existence of threshold effects or other complicating biological or physical factors (Orth *et al.* 1984). The shallower Henley Beach site shows linear relations in three out of four cases but the deeper Brighton site shows none. The likely presence at the Brighton site of organic matter in surface sediments, as suggested by the large number of detrital feeding organisms (e.g. *Lissoteia* and *Leptomysis*) in the samples from unvegetated sand, could blur such relations even if they existed. However the differences between the two sites could also be due to other factors related to depth, time of year, or simply a function of the sites themselves.

Patches of bare sand in blowouts are continuing to expand in Holdfast Bay from numerous

¹Staples D. A. Sea spiders or Pycnogonids. Unpublished ms.

TABLE 5. Mean abundances per sample of the 25 most common species in Amphibolis (A), Posidonia (P) and unvegetated sand (S) at Henley Beach (H) and Brighton (B). Data for Henley Beach are for Sites 1 and 2 combined. No reference to a habitat indicates zero abundance. Probability values are from t tests. (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Species are listed in four ecological groups according to apparent habitat preferences. Abbreviations of species are those given in Fig. 4.

Species	Abbreviation
<i>Amphibolis</i> preferring	
MOLLUSCA	
<i>Cantharidus irisodontes</i> A 2.3, P 0.3** (H,B)	Ci
<i>Cantharidus bellulus</i> A 1.4 (H,B)	Cb
<i>Bedeia paivae</i> A 2.8 (H,B)	Bp
<i>Cingulina</i> sp A 4.6, S 0.5* (B)	C sp
<i>Stenochiton cymodocealis</i> A 13 (H)	Sc
CRUSTACEA	
<i>Cerapus abdectus</i> A 13.8, P 1.3* (H,B)	Ca
<i>Tryphosella orana</i> A 12.2, P 0.5* (H)	To
<i>Parawaldeckia</i> sp A 22.9 (H)	Psp
<i>Tethygeneia</i> sp A 11.6, P 0.8** (H,B)	Tsp
<i>Lepidochelia ignota</i> A 5.5, P 0.5, S 1.2 A-S* A P* (H,B)	Li
<i>Vargula</i> sp A 17.7 (H)	Vsp
<i>Posidonia</i> preferring	
MOLLUSCA	
<i>Notoacmaea flammea</i> P 9.5 (H)	Nf
CRUSTACEA	
<i>Neonesidea</i> sp P 4.8, A 0.7* (H)	Nsp
<i>Preferring vegetated substrata (V) (combining data for Amphibolis and Posidonia) to unvegetated sand (S)</i>	
MOLLUSCA	
<i>Thalotia conica</i> V 3.8 (H,B)	Tc
<i>Macrozafra atkinsoni</i> V 6.4, S 0.2** (H,B)	Ma
<i>Musculus paulucciae</i> V 17.8 (H,B)	Mp
CRUSTACEA	
<i>Erichthonius</i> sp V 2.40 (B)	Esp
<i>Ochlesia eridunda</i> V 25.7, S 0.3*** (H,B)	Oe
<i>Porcellidium</i> sp V 8.1, S 0.4* (H,B)	Psp
Sand - preferring	
MOLLUSCA	
<i>Lissotesta contabulata</i> S 32.1 (B)	Lc
CRUSTACEA	
<i>Guernia cf gelane</i> P 1.1, S 93.9** (H)	Gg
<i>Leptomysis australiensis</i> S 2.3 (B)	La
<i>Cypridinodes cf galathea</i> A 0.5, P 2.5, S 7.3, P-S** A-S** (H)	Cg
ECHINODERMATA	
<i>Allostichaster polyplax</i> P 0.7, S 11.8* (H)	
Non-selective	
CRUSTACEA	
<i>Amphiascopsis</i> spp A 7.9, P 1.1, S 2.9 ns (B)	Ac

man-related and other causes (Clarke & Thomas in press). Immediate effects of seagrass loss on the epifauna are probably reflected in the differences we observed between the complex epifaunal assemblage in seagrasses and the quite different sand-dwelling assemblage. Longer term effects due to

loss of organic production are likely to entail widespread and serious declines in numbers of individuals and species of the epifauna that is trophically dependent on seagrass, its epiphytes or its detritus, and of fish and other secondary consumers that in turn depend for food on the epifauna.

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